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A Preliminary Enumeration of the Grasses of Porto Rico

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This enumeration is based mainly upon the material in the herbarium of the New York Botanical Garden. The collections of Heller, Underwood and Griggs, Wilson and Goll are there fully represented, and those of Sintenis partially so. A few species, of which we have not seen specimens, have been admitted upon the authority of monographers. Further explorations of the island must add more species, and it is hoped that this enumeration may serve as a help in such further exploration. That this work may be facilitated, it has been deemed advisable to incorporate analytical keys to the tribes, genera and species. This enumeration credits the island with 10 of the 13 grass tribes, 37 genera, and 75 species and varieties, among them 9 hitherto unknown.

Key to the Tribes

A. Spikelets falling from the pedicel entire, naked or enclosed in bristles or a bur-like involucre, or immersed in the internodes of a readily disarticulating rachis, 1-flowered, or if 2-flowered the lower flower staminate (perfect in *Isachne*): internodes of the rachilla of the spikelet very short, not measurable.

Spikelets round or somewhat dorsally compressed: hilum punctiform.

Flowering scale and palet hyaline, thin, much more delicate in structure than the thick-membranous to coriaceous empty scales.

Spikelets unisexual. Tribe I. MAYDEAE.

Spikelets in pairs, one sessile, the other pedicellate, the former perfect, the latter sometimes perfect, often with a staminate flower, or frequently empty, abortive or wanting. Tribe II. ANDROPOGONEAE.

Flowering scale, at least that of the perfect flower, similar in texture to the empty scales, or frequently thicker and firmer, never hyaline and thin.

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Flowering scale and palet membranous.
Inflorescence spicate. Tribe III. ZOYSIEAE.
Inflorescence paniculate. Tribe IV. TRISTEGINEAE.
Flowering scale and palet chartaceous, cartilaginous or coriaceous, very different in appearance from the remaining scales.
Tribe V. PANICEAE.
Spikelets much compressed laterally: hilum linear. Tribe VI. ORYZEAE.
B. Spikelets with the empty scales persistent, the rachilla hence articulated above them,
1–many-flowered: internodes of the rachilla of spikelets of 2 or more flowers long and readily measurable.
Stems herbaceous (except in one species of *Panicum*): leaf-blade sessile, not articulated with the sheath.
Spikelets borne in open or spike-like panicles or racemes, usually upon distinct and often long pedicels.
Spikelets 1-flowered. Tribe VII. AGROSTIDEAE.
Spikelets 2–many-flowered. Tribe IX. FESTUCEAE.
Spikelets borne in two rows, on short equal pedicels or sessile.
Tribe VIII. CHLORIDEAE.
Stems woody: leaf-blade with a petiole-like base which is articulated with the sheath. Tribe X. BAMBUSEAE.

Tribe I. MAYDEAE

A tall stout grass with the pistillate spikelets enclosed in a globose white bead-like organ. 1. *Coix*.

Tribe II. ANDROPOGONEAE

First scale of the spikelet globose, rugose: racemes not hairy. 2. *Hackelochloa*.
Scales of the spikelet long, flat or convex: racemes hairy.
Racemes singly disposed.
Second scale of the sessile spikelet awnless: pedicellate spikelet smaller than the sessile one. 3. *Schizachyrium*.
Second scale of the sessile spikelet awned: pedicellate spikelet larger than the sessile one. 4. *Diectomis*.
Racemes in pairs, or sometimes 3's–5's. 5. *Andropogon*.

Tribe III. ZOYSIEAE

A low grass with a narrow spike-like inflorescence. 6. *Anthephora*.

Tribe IV. TRISTEGINEAE

A tall grass with a large panicle of awned spikelets. 7. *Arundinella*.

Tribe V. PANICEAE

1. Spikelets all perfect: leaf-blades sessile.
a. Spikelets not sunken in the rachis.
* Spikelets naked, not involucrate.
Scales 3.
Lowest scale with a thickened ring-like callus. 8. *Monachne*.
Lowest scale unappendaged.
Flowering scale with its opening turned from the rachis. 9. *Paspalum*.

Flowering scale with its opening turned toward the rachis. 10. *Anastrophus.*

Scales 4. 11. *Isachne.*

Perfect flowers 2.

Perfect flower 1.

Second empty scale not saccate at the base.

Empty scales not awned.

Spikelets in very slender 1-sided racemes which are usually whorled or approximate. 12. *Syntherisma.*

Spikelets in panicles or panicled racemes, the latter never whorled, commonly distant.

Spikelets long-hairy, acuminate. 13. *Trichachne.*

Spikelets glabrous or with only short hairs, usually orbicular to ovate, if lanceolate glabrous.

Spikelets hemispheric, orbicular or nearly so in outline, the rachis of the 1-sided racemes winged. 14. *Dimorphostachys.*

Spikelets not hemispheric, varying in outline, usually in panicles, rarely in racemes and then the rachis not winged.

Flowering scale without lateral pits or appendages at the base. 15. *Panicum.*

Flowering scale with pits or membranous appendages at the base. 16. *Ichnanthus.*

Empty scales awned or awn-pointed.

Stems creeping: leaf-blades short and broad. 17. *Oplismenus.*

Stems erect: leaf-blades long and narrow. 18. *Echinochloa.*

Second empty scale saccate at the base. 19. *Sacciolepis.*

** Spikelets involucrate.

Involucre of bristles. 20. *Chaetochloa.*

Involucre of 2 spine-bearing valves. 21. *Cenchrus.*

b. Spikelets sunken in one side of the broad flattened rachis. 22. *Stenotaphrum.*

2. Spikelets monoecious: leaf-blades with a petiole-like base. 23. *Olyra.*

Tribe VI. ORYZEAE

Grasses with broad flat leaf-blades and long narrow spikelets. 24. *Pharus.*

Tribe VII. AGROSTIDEAE

Flowering scale with three long awns. 25. *Aristida.*

Flowering scale awnless. 26. *Sporobolus.*

Tribe VIII. CHLORIDEAE

1. Spikelets with 1 perfect flower.

Spikes digitate or in whorls.

Second empty scale acute: awn of the flowering scales usually long. 27. *Chloris.*

Second empty scale truncate or 2-toothed: flowering scales awnless or awn-pointed. 28. *Eustachys.*

Spikes scattered, single. 29. *Heterosteca.*

2. Spikelets with 2–3 perfect flowers.

Spikes usually digitate: spikelets crowded.

Spikes with terminal spikelets. 30. *Eleusine.*

Spikes with the rachis extending beyond the spikelets in a manifest point. 31. *Dactyloctenium.*

Spikes distant: spikelets alternate. 32. *Leptochloa.*

Tribe IX. FESTUCEAE

Tall grasses with large dense hairy panicles and broad flat leaf-blades.

Dioecious: staminate spikelets glabrous. 33. *Gynerium.*

Hermaphrodite: spikelets hairy. 34. *Phragmites.*

Low grasses with open glabrous panicles.

Empty scales 2: flowering scales 3-nerved. 35. *Eragrostis.*

Empty scales 3–6: flowering scales many-nerved. 36. *Uniola.*

Tribe X. BAMBUSEAE

Grasses with woody stems and the leaves often fasciculately arranged. 37. *Arthrostylidium.*

1. COIX L. Sp. Pl. 972. 1753

1. COIX LACHRYMA-JOBI L. Sp. Pl. 972. 1753.

In wet places, frequent. Between Aibonito and Cayey, Heller 528; Rio Piedras, Goll 316; Adjuntas road, near Ponce, Heller 6075.

2. HACKELOCHLOA Kuntze, Rev. Gen. 2: 776. 1891

Manisuris Sw. Prod. 25. 1788.

1. HACKELOCHLOA GRANULARIS (L.) Kuntze, Rev. Gen. Pl. 2: 776. 1891.

Cenchrus granularis L. Mant. 575. 1771.

Manisuris granularis Sw. Prod. 25. 1788.

Near Mayaguez, Heller 4401.

3. SCHIZACHYRIUM Nees, Agrost. Bras. 331. 1829

1. SCHIZACHYRIUM brevifolium (Sw.) Nees; Kunth, Enum. 1: 488. 1833.

Andropogon brevifolius Sw. Prod. 26. 1788.

Adjuntas road, near Ponce, Heller 6230.

4. DIECTOMIS H.B.K. Nov. Gen. & Sp. **1**: 193. 1815

1. DIECTOMIS FASTIGIATA (Sw.) H.B.K. Nov. Gen. & Sp. **1**: 193, *pl. 64*. 1815.

Andropogon fastigiatus Sw. Prod. 26. 1788.

Meadows on Mt. Santano, Coamo, Sintenis 3247.

5. ANDROPOGON L. Sp. Pl. 1043. 1753

Racemes not surrounded by bracts: spikelets awnless: foliage not lemon-scented.
Stems tall and stout, the inflorescence large and much-branched. 1. *A. bicornis.*
Stems low, tufted, slender, the inflorescence slender and consisting of but few branches. 2. *A. leucostachys.*
Racemes surrounded by sheathing bracts: spikelets awned: foliage lemon-scented. 3. *A. Nardus.*

1. ANDROPOGON BICORNIS L. Sp. Pl. 1043. 1753.

In dry soil, frequent. Luquillo Mts., Wilson 226; Santurce, Heller 597.

2. ANDROPOGON LEUCOSTACHYS H.B.K. Nov. Gen. & Sp. **1**: 187. 1815.

Sandy soil, frequent. Heller 933, 984 and 4396; Goll 326.

3. ANDROPOGON NARDUS L. Sp. Pl. 1046. 1753.

Santurce, Heller 229 (leaves only). The immature character of the only specimen of this grass we have seen from Porto Rico makes its definite determination impossible. In leaf character it strongly resembles this species.

6. ANTHEPHORA Schreb. Beschr. Graes. **3**: 105. 1810

1. ANTHEPHORA HERMAPHRODITA (L.) Kuntze, Rev. Gen. 759. 1891.

Tripsacum hermaphroditum L. Syst. Ed. 10, 1261. 1759.

Anthephora elegans Schreb. Beschr. Graes. **3**: 105. 1810.

In waste places, frequent. Santurce, Heller 165 and 1348.

7. ARUNDINELLA Raddi, Agrost. Bras. 37, *pl. 1*. 1823

1. ARUNDINELLA MARTINICENSIS Trin. Gram. Pan. 62. 1826.

Caguas, Heller, 934; Mayaguez, Heller, 4355; Adjuntas road, near Ponce, Heller 6256.

8. MONACHNE Beauv. Agrost. 49, *pl. 10.* 1812

Eriochloa H.B.K. Nov. Gen. & Sp. 1: 94, *pl. 30, 31.* 1815.

Rachis of the inflorescence softly pubescent with short spreading hairs: outer scales of the spikelet pubescent with many long stiff hairs. 1. *M. punctata.*

Rachis merely scabrous on the angles: outer scales less pubescent and with shorter finer hairs. 2. *M. subglabra.*

1. MONACHNE PUNCTATA (L.).

Milium punctatum L. Syst. Ed. 10, 872. 1759.

Eriochloa punctata Hamilt. Prod. 5. 1825.

Humacao, Blauner; Adjuntas road, near Ponce, Heller 6298.

2. **Monachne subglabra** sp. nov.

A tall somewhat branching grass with rather broad, flat leaf-blades. Stems 8–12 dm. long, glabrous, the nodes densely pubescent with short, spreading hairs: leaves numerous; sheaths usually shorter than the internodes and much shorter than the blades, ciliate on the margins, the lower ones papillose-hirsute between the nerves; ligule a ring of short hairs; blades linear to lanceolate, flat, ascending, or the longer ones drooping, glabrous, very rough on the margins, long-acuminate at the apex, generally narrowed toward the base, 1–3 dm. long and 7–17 mm. wide: inflorescence finally somewhat exserted, the rachis hispidulous on the ridges: racemes ascending, commonly 6–10, the larger 4–6 cm. long, the rachis hispidulous on the margins and more or less setiferous: spikelets on shorter pedicels which usually bear a few long hairs, 3.5 mm. long and about 1.3 mm. wide, elliptic to ovate-lanceolate, acute, a short semicircular first scale usually present, the second and third scales about equal in length, acute, rather sparingly pubescent with appressed hairs, 5-nerved, the third scale bearing in its axil a palet of equal length and a staminate flower, the fourth scale about three fourths as long as the spikelet, elliptic, mucronate, finely transverse-rugose.

Collected at Martin Peña January 31, 1899, by Heller, no. 380.

9. PASPALUM L. Syst. Ed. 10, 855. 1759

1. Racemes scattered along the axis of the inflorescence.

a. Spikelets broadly elliptic to orbicular, one half as wide as long; rachis of racemes manifestly wing-margined.

* Spikelets not margined.

Stems erect or nearly so, stout: leaf-blades long: outer scales of the spikelet with a midnerve.

Spikelets glabrous.

Third scale of the spikelet white or yellowish at maturity: basal

leaf-sheaths very broad and reticulated, at least when dry-
Spikelets about 1.5 mm. long: racemes numerous. 1. *P. densum.*
Spikelets about 2.5 mm. long: racemes 12-18. 2. *P. Underwoodii.*
Third scale dark brown at maturity: basal sheaths not broad nor reticulated. 3. *P. Boscianum.*
Spikelets pubescent.
Spikelets elliptic, about one half as wide as long, the pubescence appressed. 4. *P. Helleri.*
Spikelets broadly oval or obovate, the pubescence spreading.
Spikelets less than 1.5 mm. long. 5. *P. hemisphaericum.*
Spikelets 2.5–3 mm. long. 6. *P. virgatum.*
Stems slender, creeping at the base: leaf-blades short, rarely more than 5 cm. long: outer scales of the spikelet without a midnerve. 7. *P. orbiculatum.*
** Spikelets surrounded by a broad toothed margin. 8. *P. fimbriatum.*
b. Spikelets narrowly elliptic, less than one half as broad as long: rachis of racemes barely, if at all, margined. 9. *P. Portoricense.*
2. Racemes long and slender, arising in pairs at the apex of the stem, rarely with another one a short distance below. 10. *P. conjugatum.*

1. PASPALUM DENSUM Poir. in Lam. Encycl. **5**: 32. 1804.

A single specimen of this species from Porto Rico has been seen by the writer, and is the type in the herbarium of Lamarck at Paris; it was collected by Ledru.

2. **Paspalum Underwoodii** sp. nov.

A tall perennial with reticulated basal leaf-sheaths, elongated leaf-blades and rather dense inflorescence. Stems 8–12 dm. tall, erect, rather stout at the base: leaves numerous at the base; sheaths glabrous, the basal ones strongly reticulated, at least when dry, rather abruptly narrowed into the blade at or below the middle, equitant; ligule a scarious ring; blades 4–7 dm. long, about 1 cm. wide, long-acuminate at the summit, exceedingly rough on the lower surface, densely hirsute on the upper surface, serrulate on the margins: inflorescence 1.5–2.5 dm. long: racemes 12–18, sessile or nearly so, ascending or nearly erect, the lower ones 7–10 cm. long, the rachis including its serrulate wings about 1 mm. wide and more or less setiferous, usually purplish: spikelets in pairs in two rows, on short hispid pedicels, yellowish green, usually more or less purplish tinged, glabrous, broadly obovate, 2.5 mm. long, 2 mm. broad, and about 0.8 mm. thick, apiculate, the 2 outer scales 3-nerved, apiculate, the third scale yellowish-white, oval, 2.2 mm. long and about 1.7 mm. wide, minutely striate.

Type collected by Underwood and Griggs along roadsides,

Mayaguez to Joyua, June 14 to July 22, 1901, no. 149. The following specimens also belong here: Plaza de Humacao, Eggers 676, 1881; between Mayaguez and Añasco, Sintenis 1223, 1885, and near Guanica, 3412*b*, 1885, of the same collector; Santurce, Heller 594; near Mayaguez, Heller 4368.

Related to *P. densum* Poir., but that has more numerous racemes and much smaller spikelets.

3. PASPALUM BOSCIANUM Fluegge, Gram. Mon. 171. 1810.

Paspalum purpurascens Ell. Bot. S. C. & Ga. **1**: 108. 1817. El Yunque, Luquillo Mts., Wilson 43.

4. **Paspalum Helleri** sp. nov.

A tufted nearly glabrous perennial. Stems 4–8 dm. tall, finally branching above, rather slender, smooth and glabrous, the nodes glabrous: leaves usually 3; sheaths smooth and glabrous, shorter than the internodes; ligule a scarious ring about 1 mm. long; blades erect, or drooping at the end, smooth and glabrous on the surfaces with the exception of some long hairs on the upper surface just back of the ligule, the margins rough, linear, acuminate at the apex, the larger ones 1.5–2.5 dm. long and 5–7 mm. wide: racemes 2–4, sometimes single on the branches, slender, 6–9 cm. long, the rachis more or less flexuous, winged and about 1 mm. wide: spikelets in pairs, 2 mm. long and about 1 mm. wide, elliptic, obtuse, the two outer scales 3-nerved, the first scale pubescent with long weak hairs, the second one glabrous, the third scale and palet greenish.

In fields and waste places. Type collected at Santurce, Jan. 9, 1899, by Heller, no. 10. No. 164, secured by this collector at the same place, also belongs here.

5. PASPALUM HEMISPHAERICUM Poir. in Lam. Encycl. **5**: 31. 1804.

Paspalum paniculatum Gaertn. Fruct. Sem. **2**: 2, *pl. 80.* 1791. In part. Not Linnaeus.

Near Mayaguez, Heller 4399; Adjuntas road, near Ponce, Heller 6227.

6. PASPALUM VIRGATUM L. Syst. Ed. 10, 855. 1759.

In sandy soil, common. Luquillo Mts., Wilson 227; Rio Piedras, Heller 130 and 625; Cataño, Heller 1373; Underwood and Griggs 794.

7. PASPALUM ORBICULATUM Poir. in Lam. Encycl. **5**: 32. 1804.
Paspalum pusillum Vent.; Fluegge, Gram. Mon. 100. 1810.
Wet banks, south of San Juan, Heller 664.

8. PASPALUM FIMBRIATUM H.B.K. Nov. Gen. & Sp. **1**: 93, *pl. 28*. 1815.

In ditch, Coamo to Ponce, Underwood and Griggs 576; Ponce, Heller 6219.

9. **Paspalum Portoricense** sp. nov.

A low tufted nearly glabrous slender perennial. Stems about 1 dm. tall, glabrous, with the exception of a few hairs at the nodes, simple: leaves 2 or 3; sheaths glabrous, usually shorter than the internodes and shorter than the blades; ligule scarious, acute, 1–2 mm. long; blades ascending, flat, rather thin, the upper surface with some long hairs at the very base and a few scattered ones elsewhere, sparingly ciliate on the margins, the lower surface glabrous, linear, acuminate at the apex, usually more or less narrowed toward the base: inflorescence very slender, about 2 cm. long, of 1 or 2 erect branches: spikelets in pairs, one on a long and the other on a short pedicel, elliptic, 1.8 mm. long and 0.7 mm. wide, usually purplish tinged, glabrous, the first and second scales 3-nerved, the third scale greenish-white, a little shorter than the outer scales, obtuse.

Type collected between Aibonito and Cayey, February 8, 1899, by Heller, no. 524.

10. PASPALUM CONJUGATUM Berg. Act. Helv. **7**: 129, *pl. 8*. 1772.

Near Mayaguez, Heller 4397; Mayaguez to Joyua, Underwood and Griggs 175; Luquillo Mts., Wilson 159.

10. ANASTROPHUS Schlecht. Bot. Zeit. **8**: 681. 1850.

1. ANASTROPHUS COMPRESSUS (Sw.) Schlecht.; Doell. in Mart. Fl. Bras. **2**^{2}: 102. 1877.
Milium compressum Sw. Prod. 24. 1788.
Rio Blanco, Blauner.

11. ISACHNE R. Br. Prod. 196. 1810

1. **Isachne angustifolium** sp. nov.

A prostrate leafy branching perennial, forming large mats, with narrow leaf-blades and rather small panicles. Stems 1 m. long or less, glabrous or very sparingly pubescent below, the

uppermost internode minutely appressed-pubescent: leaves numerous; sheaths glabrous or sparingly hispid, papillose-ciliate on the margins, those on the main stem shorter than the internodes, those on the branches overlapping; ligule a ring of short hairs; blades erect or ascending, linear to linear-lanceolate, acuminate, rough and green on the upper surface, smooth and glaucous on the lower surface, the lower the shorter, only 2–3 cm. long, increasing in length toward the summit where they are 5–10 cm. long and 4–6 mm. wide: panicles long-exserted, 5–8 cm. long, their main axis and widely spreading primary branches minutely pubescent, the secondary branches similarly pubescent and at an angle of about 45° with the primary branches: spikelets about 1.5 mm. long, on shorter pedicels, the two outer scales about equal in length, equalling or a little shorter than the spikelet and sparingly pubescent at the apex, obtuse, the first broadly oval, the second almost orbicular, the two flowering scales glabrous, yellowish, about 1.3 mm. long.

On the summit of El Yunque, Luquillo Mountains, Porto Rico, Wilson, no. 160.

12. SYNTHERISMA Walt. Fl. Car. 76. 1788

Spikelets one quarter as wide as long or more, acute, the fourth scale yellowish when mature. 1. *S. fimbriatum.*

Spikelets one fifth as wide as long, acuminate, the fourth scale greenish when mature. 2. *S. setosum.*

1. SYNTHERISMA FIMBRIATUM (Link) Nash, Bull. Torrey Club, **25**: 302. 1898.

Digitaria fimbriata Link, Hort. Berol. **1**: 226. 1827.

Waste places, common. Cataño, Heller 107, and Bayamon, Heller 422.

2. SYNTHERISMA SETOSUM (Desv.) Nash, Bull. Torrey Club, **25**: 300. 1898.

Digitaria setosa Desv.; Hamilt. Prod. 6. 1825.

Near Mayaguez, Heller 4398.

13. TRICHACHNE Nees, Agrost. Bras. 85. 1829

1. TRICHACHNE INSULARE (L.) Nees, Agrost. Bras. 86. 1829.

Andropogon insularis L. Syst. Ed. 10, 1304. 1759.

Panicum leucophaeum H.B.K. Nov. Gen. & Sp. **1**: 97. 1815.

In fields and along streams, frequent. Heller 136 and 650; Underwood and Griggs 131 and 564; Goll 479; Adjuntas road, near Ponce, Heller 6158.

14. DIMORPHOSTACHYS Fourn. Comptes-Rendus Acad. Par. **80**: 441. 1875

1. DIMORPHOSTACHYS PEDUNCULATA (Poir.) Fourn. Mex. Pl. **2**: 15. 1886.

Paspalum pedunculatum Poir. in Lam. Encycl. Suppl. **4**: 315. 1816.

Adjuntas road, near Ponce, Heller 6354.

15. PANICUM L. Sp. Pl. 55. 1753

1. Apex of the panicle-branches not extending beyond the insertion of the spikelets.
   a. Stems herbaceous.
      Spikelets scattered, on long pedicels of varying length.
         Fourth scale of the spikelet smooth: low grasses, less than 5 dm. tall.
            Panicle large and effuse, over 1 dm. long: spikelets numerous, less than 1.5 mm. long.
               Leaf-blades narrowly ovate, rarely exceeding 7 cm. long: spikelets 1 mm. long. 1. *P. brevifolium.*
               Leaf-blades lanceolate, rarely less than 1 dm. long: spikelets 1.3 mm. long. 2. *P. trichanthum.*
            Panicle small, less than 1 dm. long: spikelets few, 1.5 mm. long or more.
               Stems erect, if prostrate in age never rooting at the lower nodes.
                  Spikelets less than 2 mm. long.
                     Leaf-blades with the upper surface hirsute, the larger over 1 cm. wide. 3. *P. comophyllum.*
                     Leaf-blades with the upper surface glabrous or merely puberulent, less than 5 mm. wide. 4. *P. Nashianum.*
                  Spikelets more than 2 mm. long. 5. *P. consanguineum.*
               Stems erect only toward the end, the base prostrate and rooting at the lower nodes.
                  Leaf-blades lanceolate, pubescent, less than 5 mm. wide. 6. *P. parvifolium.*
                  Leaf-blades ovate-lanceolate, more than 5 mm. wide. 7. *P. oplismenoides.*
         Fourth scale of the spikelet transversely rugose: tall stout grasses. 8. *P. maximum.*
      Spikelets crowded on short nearly equal pedicels, in short clusters on one side of the panicle-branches.
         Outer scales of the spikelet with cross-veinlets connecting the longitudinal nerves. 9. *P. paniculatum.*
         Outer scales without cross-veinlets.
            Fourth scale of the spikelet transversely rugose.
               Spikelets about 2 mm. long: stems slender: leaf-blades ovate-lanceolate, usually less than 5 cm. long. 10. *P. prostratum.*

Spikelets about 3 mm. long: stems stout: leaf-blades long and linear. 11. *P. molle.*

Fourth scale of the spikelet smooth. 12. *P. laxum.*

b. Stems woody, bamboo-like. 13. *P. latifolium.*

2. Apex of the panicle-branches extending beyond the insertion of the spikelets in an awn-like appendage.

Second scale of the spikelet 3-nerved, the fourth scale smooth. 14. *P. Sintenisii.*

Second scale of the spikelet 5–7-nerved, the fourth scale transversely rugose. 15. *P. flavescens.*

1. PANICUM BREVIFOLIUM L. Sp. Pl. 59. 1753.

In fields and waste places, frequent. Santurce, Heller 157; Martin Peña, Heller 387; Luquillo Mts., Wilson 283; Adjuntas road, near Ponce, Heller 6094.

2. PANICUM TRICHANTHUM Nees, Agrost. Bras. 210. 1829.

In moist ground, between Aibonito and Cayey, Heller 531.

3. **Panicum comophyllum** sp. nov.

A tufted densely pubescent perennial, finally much-branched, with broad flat leaf-blades and rather large panicles. Stems 3–4 dm. tall, hirsute with long ascending hairs: leaves 5–7; sheaths densely hirsute with spreading hairs, the primary ones shorter than the internodes and the blades; ligule a ring of stiff hairs about 2 mm. long; blades spreading or ascending, flat, softly hirsute on both surfaces with spreading hairs, those on the upper surface the longer, ciliate on the margin with stiffer hairs; those on the main stem oblong-linear to ovate-lanceolate, acute, barely cordate at the somewhat clasping base, 5–7 cm. long, 10–13 mm. wide: panicle somewhat exserted, 5–7 cm. long and about as broad, broadly ovate, the main axis pubescent with short spreading hairs, its branches somewhat ascending: spikelets broadly obovate, 1.5 mm. long and about 1 mm. wide, pubescent with spreading hairs.

Type collected in rich soil at Santurce, January 9, 1899, by Heller, no. 12.

Related to *P. ciliosum* Nash, of the southern United States, but readily distinguished by its softly pubescent leaf-blades.

4. PANICUM NASHIANUM Scribn. Bull. U. S. Dept. Agric. Div. Agrost. 7: 79. 1897.

In sand, quite common. Vega Baja, Heller, 639; Manati to

Vega Baja, Underwood and Griggs 955; Santurce, Heller 982*b* and 6442.

5. PANICUM CONSANGUINEUM Kunth, Rev. Gram. **1**: 36. 1829.
Sandy soil, Santurce, Heller 982.

6. PANICUM PARVIFOLIUM Lam. Ill. **1**: 173. 1791.
Bayamon, Sintenis 1216.

7. **Panicum oplismenoides** sp. nov.

A smooth and glabrous prostrate leafy perennial with much of the habit of *Oplismenus setarius*, with short broadly lanceolate leaf-blades and spreading panicles. Stems slender, rooting at the lower nodes, branching: leaves numerous; sheaths much shorter than the internodes and about one half as long as their blades; ligule a very narrow scarious ring; blades spreading, shorter than the internodes, broadly lanceolate to ovate-lanceolate, often somewhat undulate on the margins, 2–3 cm. long, 6–10 mm. wide: panicles but little exserted, broadly ovate, 3–4 cm. long, the branches spreading: spikelets elliptic, 1.8–2 mm. long and a little less than 1 mm. broad, the first scale a little more than one half as long as the spikelet, 5-nerved, broadly ovate, obtuse, the second and third about equal in length, 5-nerved, a little exceeding the white flowering scale, the third scale with a manifest palet nearly as long as itself.

Collected on the edge of a ditch at Vega Baja, May 9, 1899, by Heller, no. 1316.

Related in habit and general appearance to *P. polygonoides* Lam., but in that the leaf-blades are smaller and with hispid sheaths and the spikelets globular.

8. PANICUM MAXIMUM Jacq. Ic. Pl. Rar. **1**: 13. 1781–6.
Martin Peña, Heller 377; Martin Peña and Lecheria, Goll 31.

9. **Panicum paniculatum** (L.).
Paspalum paniculatum L. Syst. Ed. 10, 855. 1759.
Panicum fasciculatum Sw. Prod. 22. 1788.
In sandy and rocky soil, frequent. Rio Piedras, Heller 135; Aguadilla, Heller 4528; Sprengel; H. Wydler 311; Adjuntas road, near Ponce, Heller 6226 and 6302.

It may be of interest to note here that the specimen from which Sloane's figure (Hist. Jam. *pl. 72, f. 2*) was drawn, and on which Linnaeus based his *Paspalum paniculatum*, has been examined by

the writer, and that it is what is commonly known as *Panicum fasciculatum* Sw.

10. PANICUM PROSTRATUM Lam. Ill. 1: 171. 1791.

Cane field between Ponce and Coamo, Heller 497.

11. PANICUM MOLLE Sw. Prod. 22. 1788.

Along railroad, Bayamon, Heller 100; Yauco, Heller 6293.

12. PANICUM LAXUM Sw. Prod. 23. 1788.

In fields, common. Between Aibonito and Cayey, Heller 522; Santurce, Heller 983; Cataño, Heller 1378.

13. PANICUM LATIFOLIUM L. Sp. Pl. 58. 1753.

In woods and thickets, common. Maricao, Sintenis 215; Mayaguez, Heller 4375; Arecibo, Heller 343; Luquillo Mts., Wilson 350; Coamo, Goll 699; Bayamon, Goll 227.

14. **Panicum Sintenisii** sp. nov.

A tufted glabrous perennial with long narrow flat leaf-blades and a slender panicle. Stem 4–6 dm. tall, slender, producing panicle-bearing branches from the upper sheaths: leaves about 4; sheaths several times shorter than the internodes and the blades; ligule a ring of short hairs; blades narrow and elongated, flat toward the apex, but folded below for a considerable distance, at least when dry, giving the blade a long-stalked appearance, 1–2 dm. long and about 2 mm. wide at the flat portion, the lower folded portion about one quarter this width, long-acuminate: panicle very slender, 4–7 cm. long, its branches appressed, 1–2 cm. long, each running out into a bristle-like termination as do its divisions: spikelets about 2 mm. long, acute, as are also all the scales, the first scale 1-nerved, about one half as long as the spikelet, the second one 3-nerved, about two thirds as long as the spikelet, the third scale 5-nerved and equalling the fourth scale or a little shorter than it, the fourth scale very acute.

In woods, Guanica, Sintenis 3463.

Related to *P. Chapmani* Vasey, but that has stouter spikelets and all the scales with more nerves.

15. PANICUM FLAVESCENS Sw. Prod. 23. 1788.

Near Mayaguez, Heller 4373 and 4488.

16. ICHNANTHUS Beauv. Agrost. 56, *pl. 12, f. 1.* 1812

1. ICHNANTHUS PALLENS (Sw.) Munro; Benth. Fl. Hongk. 414. 1861.

Panicum pallens Sw. Prod. 23. 1788.

In wet shaded places, common. Bayamon, Heller 92; Santurce, Heller 826; Mayaguez, Heller 4374 and 4479; Puente Fluco, Goll 884; Adjuntas road, near Ponce, Heller 6093.

17. OPLISMENUS Beauv. Fl. Owar. **2**: 14, *pl. 68.* 1807

1. OPLISMENUS SETARIUS (Lam.) R. & S. Syst. **2**: 481. 1817.

Panicum setarium Lam. Ill. **1**: 170. 1791.

In moist soil, frequent. Piñon, Goll 623; Adjuntas road, near Ponce, Heller 6303.

18. ECHINOCHLOA Beauv. Agrost. 53, *pl. 11, f. 11.* 1812.

1. ECHINOCHLOA COLONA (L.) Link, Hort. Berol. **2**: 209. 1833.

Panicum colonum L. Syst. Ed. 10, 870. 1759.

In fields and waste places, common. Cataño, Heller 108; Mayaguez, Heller 4409; Coamo Springs, Goll 660.

19. SACCIOLEPIS Nash, in Britt. Man. 89. 1901.

1. **Sacciolepis striata** (L.).

Holcus striatus L. Sp. Pl. 1048. 1753.
Panicum striatum Lam. Ill. **1**: 172. 1791.
Panicum gibbum Ell. Bot. S. C. & Ga. **1**: 116. 1817.
Sacciolepis gibba (Ell.) Nash, in Britt. Man. 89. 1901.

Wet ground, near Santurce, Heller 1363.

20. CHAETOCHLOA Scribn. Bull. U. S. Dept. Agric. Div. Agrost. 4: 38. 1897

Setae at the base of the spikelet 5 or more, involucrate, antrorsely scabrous.
  Setae short, not more than twice as long as the spikelet: inflorescence usually slender. 1. *C. purpurascens.*
  Setae longer; inflorescence stout. 2. *C. imberbis.*
Setae 1–3 at the base of each spikelet, not involucrate, retrorsely scabrous above, antrorsely below. 3. *C. scandens.*

1. CHAETOCHLOA PURPURASCENS (H.B.K.) S. & M. Bull. U. S. Dept. Agric. Div. Agrost. 21: 13. 1900.

Setaria purpurascens H.B.K. Nov. Gen. & Sp. 1: 110. 1815.

In fields and waste places, frequent. Santurce, Heller 14 and 329.

2. CHAETOCHLOA IMBERBIS (Poir.) Scribn. Bull. U. S. Dept. Agric. Div. Agrost. 4: 39. 1897.

Panicum imberbe Poir. in Lam. Encycl. Suppl. 4: 272. 1816.

Sintenis 208 (*fide* Scribn. & Merr. l. c.); Adjuntas road, near Ponce, Heller 6240.

CHAETOCHLOA IMBERBIS GENICULATA (Lam.) S. & M. Bull. U. S. Dept. Agric. Div. Agrost. 21: 12. 1900.

Panicum geniculatum Lam. Encycl. 4: 727. 1797.

Differs from the species in having stouter geniculate stems, broader leaf-blades, and a longer inflorescence.

Humacao, Blauner 233.

3. CHAETOCHLOA SCANDENS (Schrad.) S. & M. Bull. U. S. Dept. Agric. Div. Agrost. 21: 17. 1900.

Setaria scandens Schrad., Schult. Mant. 2: 279. 1824.

Sintenis 6498 (*fide* Scribn. & Merr. l. c.).

21. CENCHRUS L. Sp. Pl. 1049. 1753

Involucres 4-6-flowered, armed at the base with erect barbed bristles. 1. *C. echinatus.*

Involucres 2-flowered, armed at the base with generally shorter reflexed spines. 2. *C. tribuloides.*

1. CENCHRUS ECHINATUS L. Sp. Pl. 1050. 1753.

In sandy waste places, common. Santurce, Heller 3 and 1346; Cayey, Underwood and Griggs 406.

2. CENCHRUS TRIBULOIDES L. Sp. Pl. 1050. 1753.

Fajardo, Blauner 242.

22. STENOTAPHRUM Trin. Fund. Agrost. 175. 1820

1. STENOTAPHRUM SECUNDATUM (Walt.) Kuntze, Rev. Gen. 794. 1891.

Ischaemum secundatum Walt. Fl. Car. 249. 1788.

Roadside near Bayamon, Heller 1241; in sand, Manati to Vega Baja, Underwood and Griggs 959.

23. OLYRA L. Syst. Ed. 10, 1261. 1759

1. OLYRA LATIFOLIA L. Syst. Ed. 10, 1261. 1759.
Near Mayaguez, Heller 4443 and 4583.

24. PHARUS P. Br. Hist. Jam. 344. 1756

1. PHARUS BRASILIENSIS Raddi, Agrost. Bras. 21. 1823.
Rio Blanco, Blauner; ravine, Coamo Springs, Underwood and Griggs 505 and 845.

25. ARISTIDA L. Sp. Pl. 82. 1753

1. ARISTIDA DISPERSA Trin. & Rupr. Mem. Acad. Sci. St. Petersb. VI. **7**: 129. 1829.
Guanica, Sintenis 3766.

26. SPOROBOLUS R. Br. Prod. 169. 1810

Stems tufted, not arising from rootstocks.
Spikelets about 2 mm. long, the second scale half as long or less. 1. *S. Indicus.*
Spikelets about 3 mm. long, the second scale fully as long. 2. *S. purpurascens.*
Stems arising from long branching rootstocks. 3. *S. Virginicus.*

1. SPOROBOLUS INDICUS (L.) R. Br. Prod. 170. 1810.
Agrostis Indica L. Sp. Pl. 63. 1753.
In sandy soil, common. Santurce, Heller 985 and 1275; Lecheria, Goll 22.

2. SPOROBOLUS PURPURASCENS (Sw.) Hamilt. Prod. 5. 1825.
Agrostis purpurascens Sw. Prod. 25. 1788.
Near Mayaguez, Heller 4590.

3. SPOROBOLUS VIRGINICUS (L.) Kunth, Rev. Gram. **1**: 67. 1829.
Agrostis Virginica L. Sp. Pl. 63. 1753.
On sand dunes and in sandy soil, frequent. Santurce, Heller 1412; Maunabo, Sintenis 5084.

27. CHLORIS Sw. Prod. 25. 1788.

Spikes slender: flowering scale lanceolate, not long-ciliate. 1. *C. radiata.*
Spikes stout: flowering scale oval, long-ciliate on the margins above. 2. *C. Paraguiensis.*

1. CHLORIS RADIATA Sw. Prod. 26. 1788.
In moist soil and waste places, common. Cataño, Heller 109;

Rio Piedras, Heller 195 and 196; Bayamon, Underwood and Griggs 883; Santurce, Heller 6380.

2. CHLORIS PARAGUIENSIS Steud. Syn. Pl. Gram. 204. 1855.

Chloris barbatum Sw. Fl. Ind. Occ. **1**: 200. 1797. Not *Andropogon barbatum* L. Amoen. Acad. **5**: 412. 1759.

Near Mayaguez, Heller 4417.

28. EUSTACHYS Desv. Nouv. Bull. Soc. Philom. **2**: 188. 1810

1. EUSTACHYS PETRAEA (Sw.) Desv. Nouv. Bull. Soc. Philom. **2**: 189. 1810.

In sand, Vega Baja, Heller 131; Santurce, Heller 6422.

29. HETEROSTECA Desv. Nouv. Bull. Soc. Philom. **2**: 188. 1810

1. **Heterosteca rhadina** sp. nov.

Stems tufted, 2.5–4 dm. long, slender, finally prostrate at the base and branching above: leaves several; sheaths strongly nerved, glabrous, or the lower ones sometimes more or less pubescent; ligule a narrow scarious ring; blades flat, narrowly linear, acuminate, more or less hirsute on both surfaces, especially on the upper, less than 1 dm. long, 1–2 mm. wide: spikes 3–7, short, spreading or reflexed, of 1–3 spikelets, the 3-angled rachis hispidulous on the angles, its internodes long, usually exceeding one half the length of the empty scales: spikelets distant, appressed to the rachis, the purple empty scales very acute, 1-nerved, hispidulous on the stout midrib, the first shorter than the second which is 5–6 mm. long, the first flowering scale 3-nerved, the nerves extending into short awns, the lateral ones barely reaching the apex of the body of the scale, the central one extending about 1 mm. beyond it, enclosing a perfect flower and a palet longer than its body, the second flowering scale likewise 3-nerved, the nerves extending into hispidulous awns longer than the body, enclosing a staminate flower and a longer palet.

Collected on the Adjuntas road, near Ponce, by Heller, no. 6057, and distributed as *Bouteloua Americana* (Sw.) Scribn. The *Aristida Americana* cited in the synonymy of *Bouteloua litigiosa* Lag. by Grisebach (Fl. Brit. W. I. 537) is accredited to Swartz (Obs. Bot. *t. 2, f. 2*). Swartz, however, distinctly indicates there the real authorship of the species by quoting the original Linnaean

description in the Systema Naturae. Both authors refer the plant to Jamaica, so that the plate and description of Swartz may in all probability be safely taken as characterizing the Linnaean plant also. The genus *Heterosteca* was founded by Desvaux on one species, *H. juncifolia*. At a later date he probably became acquainted with the *Aristida Americana* Sw., for in a subsequent publication (Jour. de Bot. **3**: 68. 1813) he changes the name to *Heterosteca Americana*, citing *H. juncifolia* as a synonym.

The plant of Swartz is quite different from the one we have under consideration, differing in the more numerous spikes with more spikelets, and in the second flowering scale being reduced to a 3-awned empty rudiment.

30. ELEUSINE Gaertn. Fruct. **1**: 7. 1788

1. ELEUSINE INDICA (L.) Gaertn. Fruct. **1**: 8. 1788.

Cynosurus Indicus L. Sp. Pl. 72. 1753.

In cultivated and waste ground, common. Cataño, Heller 110; between Ponce and Coamo, Heller 499; Mayaguez, Heller 4410; Lecheria, Goll 20.

31. DACTYLOCTENIUM Willd. Enum. 1029. 1809

1. DACTYLOCTENIUM AEGYPTIUM (L.) Willd. Enum. 1029. 1809.

Cynosurus Aegyptius L. Sp. Pl. 72. 1753.

In cultivated and waste grounds, common. Santurce, Heller 155; Mayaguez, Heller 4411; Guanica, Sintenis 3469; Guayama, Goll, 513; Coamo Springs, Goll 661; Bayamon, Underwood and Griggs 900.

32. LEPTOCHLOA Beauv. Agrost. 71, *pl. 15, f. 1.* 1812

1. LEPTOCHLOA VIRGATA Beauv. Agrost. 166. 1812.

Moist ground near Añasco, Heller 4535.

33. GYNERIUM H. & B. Pl. Aequin. **2**: 112, *pl. 115.* 1809

1. GYNERIUM SACCHAROIDES H. & B. Pl. Aequin. **2**: 112, *pl. 115.* 1809.

Along streams, Yauco, Underwood and Griggs 718.

34. PHRAGMITES Trin. Fund. Agrost. 134. 1820

1. PHRAGMITES OCCIDENTALIS (Sieb.) Trin.; Steud. Nomen. Ed. 2, **2**: 324. 1841.

Arundo occidentalis Sieb.; Schult. Mant. **2**: 289. 1824.

Near Guanica, Heller 6289. This specimen is doubtfully referred here, its immaturity preventing a more definite determination. It was distributed as *Arundo Donax;* it hardly appears to be that plant, however. It may only be a form of the world-wide *P. Phragmites.* Mature flowering specimens of this are greatly desired.

35. ERAGROSTIS Beauv. Agrost. 70, *pl. 14, f. 11.* 1812

Flowers perfect: stems not rooting at the lower nodes.
Palet long-ciliate on the margins: panicle narrow and spike-like. 1. *E. ciliaris.*
Palet not long-ciliate: panicle loose and open.
Annual: leaf-blades less than 1 dm. long. 2. *E. Purshii.*
Perennial: leaf-blades more than 1 dm. long. 3. *E. Elliottii.*
Flowers dioecious: stems creeping. 4. *E. hypnoides.*

1. ERAGROSTIS CILIARIS (L.) Link, Hort. Berol. **1**: 192. 1827.

Poa ciliaris L. Syst. Ed. 10, 875. 1759.

In waste and cultivated soil, common. Bayamon, Heller 101; Santurce, Heller 156 and 6404; Cabo Rojo, Sintenis 838; Bayamon, Underwood and Griggs 895; Ponce, Heller 6218.

2. ERAGROSTIS PURSHII Schrad; Shlecht. Linnaea, **12**: 451. 1838.

Rio Piedras, Heller 197; between Aibonito and Cayey, Heller 551; Montellano, Goll 473; Adjuntas road, near Ponce, Heller 6198. These specimens are doubtfully referred here.

3. ERAGROSTIS ELLIOTTII S. Wats. Proc. Am. Acad. **25**: 140. 1890.

Poa nitida Ell. Bot. S. C. & Ga. **1**: 162. 1817. Not Lam. 1791.

Eragrostis nitida Chapm. Fl. S. U. S. 564. 1860.

Moist sandy soil, Santurce, Heller 584.

4. ERAGROSTIS HYPNOIDES (Lam.) B.S.P. Prel. Cat. N. Y. 69. 1888.

Poa hypnoides Lam. Ill. 185. 1791.

Roadsides, Rio Piedras, Heller, 649; Bayamon, Sintenis 1225.

36. UNIOLA L. Sp. Pl. 71. 1753

1. UNIOLA RACEMIFLORA Trin. Bull. Sc. Acad. St. Petersb. **1**: 68. 1836.

Near Salinas de Cabo Rojo, Sintenis 839.

37. ARTHROSTYLIDIUM Rupr. Mem. Acad. St. Petersb. VI. **5**: 117. 1839

Leaf-blades very narrowly linear or hair-like. 1. *A. capillifolium.*
Leaf-blades lanceolate. 2. *A. multispicatum.*

1. ARTHROSTYLIDIUM CAPILLIFOLIUM Griseb. Mem. Am. Acad. II. **8**: 531. 1863.

Near Sabanagrande, climbing on tall trees, Sintenis 3891.

2. ARTHROSTYLIDIUM MULTISPICATUM Pilger in Urban, Symb. Ant. **2**: 341. 1901.

In woods near Maricao and Adjuntas, Sintenis 209 and 4016 (according to Pilger).

A number of other specimens of the Bambuseae are in collections, but they are without inflorescence and so undeterminable.

NEW YORK BOTANICAL GARDEN.

On the Physiological Action of some of the Heavy Metals in Mixed Solutions*

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It has been shown by several investigators that, in mixed solutions containing the lighter metals, the physiological action of the electro-positive elements may in a degree antagonize each other, and a mixture of several toxic solutions of these compounds may be much less harmful than any one of the constituents taken singly. Researches concerning the physiology of sea-water have shown this to be conspicuously the case. Work on soil-solutions by Kearney and Cameron † has developed a similar situation.

The neutralizing action of the various ions on those of the heavy metals has been less studied and the present paper presents, in a preliminary way, results gained from a series of experiments performed during the summer of 1902 in the Plant Physiological Laboratory at Wood's Hole, Massachusetts.

As a test object, the primary radicle of seedlings of *Lupinus albus* was used. The method of procedure consisted essentially in suspending the seedlings on glass rods for at least 24 hours in each experiment, in such a manner as to immerse the radicles in the solution under study. In most cases the seedlings were under observation for 48 hours. At least four seedlings were used in each experiment of a series, and our deductions were drawn from the figures for average growth. With only a very few exceptions each member of the quartette manifested the same tendency. The solutions were carefully prepared from pure chemicals and were believed to be very accurate. The experiments were made in beakers.

In order to get a basis for comparison, we made a number of solutions of different compounds of each of the heavy metals used,

* Read by title at the meeting of the Botanical Society of America, held at Washington, D. C., December, 1902.

† Kearney, T. H., and Cameron, F. K. Some Mutual Relations between Alkali Soils and Vegetation. U. S. Dep. Agric. Rep. No. 71. 1902.

and determined the strongest concentration in which the plants were able to make appreciable growth. This point of undoubted growth furnished a point of departure in making comparisons. The

TABLE I

SIMPLE SOLUTIONS.* HEAVY METALS. AVERAGE GROWTH-RATES IN MILLIMETERS †

Conc. Gm. Mol.	$CuSO_4$	$CuCl_2$	$Cu(CH_3CO_2)_2$	$AgNO_3$	$HgCl_2$	$ZnSO_4$
m/8192					2.0	6.0
m/16384	0.5	1.0	1.0		9.0	9.0
m/32768	1.0	1.0	2.0		13.0	18.0
m/65536	3.5	3.0	3.0	2.0	16.0	18.0
m/131072	11.0	10.5	11.0	6.0		16.0
m/262144		16.0	15.0	13.5		
m/524288				22.0		
Check.	14.0	14.0	12.0	12.5	15.0	15.5

* All control experiments in this and subsequent series were made in water which had been very carefully distilled several times. All of the solutions were prepared from distilled water obtained under constant conditions.

† The growth-rates recorded in these tables are those for the first 24 hours.

accompanying tables give the average growth-rates at the end of twenty-four hours.

Table I summarizes the growth-rates obtained in a series of solutions of salts of copper, silver, mercury and zinc. In order

TABLE II

SIMPLE SOLUTIONS. LIGHT METALS AND UREA. AVERAGE GROWTH-RATES IN MILLIMETERS

Conc. Gm. Mol.	NaCl	Na_2SO_4	KCl	KNO_3	$Ca(NO_3)_2$	$CaCl_2$	$CaSO_4$	$MgCl_2$	Urea
m/8						1.5			0.5
m/16	2.5					9.6			1.0
m/32	3.5	1.3	0.7	3.4	20.0	16.0			3.5
m/64	7.5	1.0	2.0	4.0	20.5		35.0		8.0
m/128	13.5	2.8	6.6	8.0	21.0				
m/256		5.8	7.0	9.0	21.0				
m/512								5.5	
m/1024								6.2	
m/2048								9.4	
m/4096								12.5	
Check.	15.5	10.0	10.0	14.0	10.0	12.5	13.0	10.0	15.2

to test the possible antagonizing influence of compounds with other bases, a number of salts of sodium, potassium, calcium and magnesium were used.

A similar point indicating the maximum concentration per-

mitting growth was obtained for each of the salts of the lighter metals taken. This was necessary in order to get some idea of the permissible concentrations in which the latter might be used. Table II presents in brief the growth-rates made by the lupine roots in solutions of the salts of the second group of metals (and of urea).

SIMPLE MIXTURES

Knowing now the effect, on the growth-rate, of the heavy metals under study, also that of the salts of the lighter metals which were made use of, we have a basis for ascertaining the action of these compounds when their solutions are mixed. The method of procedure in this connection consisted briefly in mixing, with a series of graded solutions of the heavy metals, a definite quantity of the salts of the lighter metals. Two general classes of salts could be chosen for this purpose; first, those in which a common anion occurs in combination with the different cations made use of; second, salts in which also the anions differed. By making up solutions molecularly, as was done in every case, a comparison of results obtained from the same cations, combined in the two ways indicated, would enable us to judge of the action of the anions.

Table III summarizes growth-results obtained by growing lupine radicles in a series of solutions of copper salts mixed with salts of one lighter base in varying degrees of concentration. The growth-rates obtained are directly comparable to those resulting from the action of the simple solutions of the heavy metals. It will be noted that when copper sulphate is mixed with calcium sulphate, the latter containing $m/144$ grams per liter, a corresponding growth-rate is found in the case of the simple solution (Table II) at a concentration of copper sulphate indicated by $m/65536$, and in the case of the mixed solution (Table III) at a concentration of $m/16384$. These facts indicate that the presence of the given amount of calcium sulphate enables the plant to withstand four times as much copper as it was able to withstand when the latter occurred in simple solution. A further inspection of the tables shows that when calcium sulphate is present in weaker solutions, the antagonizing action is still strong, even when calcium sulphate is present in a concentration of $m/512$.

When to copper chloride, magnesium chloride is added in a

series of graded concentrations, an inspection of the tables shows that in general little, if any, diminution in the toxic action of the copper follows. This seems to indicate that magnesium is not able to diminish the poisonous action of the copper under the conditions present.

When to copper chloride, calcium chloride is added in the proportion of *m*/128, a decided decrease in the killing power of the copper is seen. When to copper chloride, sodium chloride, *m*/16, is added, a strikingly reversed situation appears. Not only is the harmful action of the copper not diminished, but the mixture seems to be slightly more poisonous than the simple copper solution or

TABLE III

MIXED SOLUTIONS. HEAVY METAL AND LIGHT METAL. COMMON ANIONS. AVERAGE GROWTH-RATES IN MILLIMETERS

Concent. of Solution of Heavy Metal	$CuSO_4 + CaSO_4$			$CuCl_2 + MgCl_2$			$CuCl_2$ + $CaCl_2$	$CuCl_2$ + NaCl	$AgNO_3$ + KNO_3	$HgCl_2$ + $CaCl_2$	$ZnSO_4$ + $CaSO_4$
	$CaSO_4$ *m*/144	$CaSO_4$ *m*/256	$CaSO_4$ *m*/512	$MgCl_2$ *m*/128	$MgCl_2$ *m*/256	$MgCl_2$ *m*/512	*m*/128	*m*/16	*m*/256		*m*/256
m/2048		0.0	0.0								33.5
m/4096	0.0	0.0	0.0							0.0	39.0
m/8192	0.0	0.0	1.0					0.0		0.0	37.5
m/16384	3.0	3.0	1.5	1.0	2.0	2.0	2.0	0.0		1.0	37.0
m/32768	8.5	7.0	3.5	1.0	3.0	1.0	6.0	0.0	1.0	2.0	
m/65536	14.0	17.0	14.0	4.0	4.0	3.0	10.5	0.5	3.0	8.0	
m/131072		19.5				5.0	15.0	1.0	5.0		
Check in water	12.0	11.0	11.0	10.0	14.0	12.0	14.5	12.0	11.5	12.0	13.0
Check in Solution of Light Metal	29.0	26.5	26.0	4.0	9.0	4.5	20.0	1.0		24.5	35.0

the simple sodium solution. This would seem to indicate that to the poisonous action of the copper that of the sodium chloride itself is added.

When to a solution of silver nitrate a solution of potassium nitrate, *m*/256, is added, no very marked change in the action of the heavy metal is noticeable, the growth-rate coinciding approximately with that seen in the solution of the pure silver salt. What difference there is seems to be in the direction of greater toxicity.

When to mercuric chloride, calcium chloride, *m*/256, is added

no diminution in the poisonous action of the corrosive sublimate is seen. Indeed, the mixture is markedly more poisonous than the solution of the simple salt. Zinc sulphate gives a very different result when calcium sulphate, *m*/256, is added. Whereas growth is much retarded in a *m*/8192 solution of zinc sulphate, in the mixture at *m*/2048 growth is more than twice as rapid as in the control grown in water. We have here a very marked stimulation in the growth-rate, resulting from the addition of the lighter metal to the zinc.

When to salts of the heavy metals compounds of the lighter

TABLE IV

MIXED SOLUTIONS. HEAVY METAL AND LIGHT METAL. DIFFERENT ANIONS. AVERAGE GROWTH-RATES IN MILLIMETERS

Concent. of Solution of Heavy Metal	$CuSO_4$ + $CaCl_2$ *m*/128	$CuSO_4$ + $CaCl_2$ *m*/128(dup.)	$Cu(CH_3CO_2)_2$ + $Ca(NO_3)_2$ *m*/32	$HgCl_2$ + $Ca(NO_3)_2$ *m*/32	$CuSO_4$ + Urea *m*/64
m/4096				0.0	
m/8192			2.0	1.0	
m/16384	1.5	3.0	5.0	6.0	
m/32768	3.0	4.0	9.5	16.0	0.0
m/65536	7.0	10.0			0.5
m/131072		16.5			4.5
Check	12.0	15.5	13.0	14.0	11.5

metals are added, in the form of salts in which the anion differs from that in the copper compound, a condition of things is found which is not essentially different from that just cited. In Table IV results bearing on this point are presented.

It will be noted that when calcium chloride, *m*/128, is added

TABLE V

MIXED SOLUTION. COPPER SULPHATE WITH CANE SUGAR. AVERAGE GROWTH-RATES IN MILLIMETERS

Concent. of Copper Solution	Cane Sugar 2*m*	Cane Sugar *m*	Cane Sugar *m*/2	Cane Sugar *m*/4	Cane Sugar *m*/8	Cane Sugar *m*/16	Check in Water
m/65536	0.0	2.7	4.0	7.5	5.5	6.5	15.5

to copper sulphate, a marked diminution in the poisonous action of the copper compound takes place to a degree equal to that seen when the anions are similar. When to copper acetate cal-

cium nitrate, $m/164$, is added, a similar situation results. In the case of solutions of mercuric chloride to which calcium nitrate has been added, we find no amelioration of the poisonous action of the corrosive sublimate, the growth being, if anything, less in the mixed solution than in that of the mercuric chloride alone.

In view of what has been said, the question naturally arises as to the effect of non-electrolytes in solution with the heavy metals. In this connection but two compounds were studied: cane sugar and urea. Tables IV and V present the results obtained. It will be seen that in a solution of copper sulphate, $m/65536$, to which cane sugar in concentrations varying from m to $m/16$ has been added, the growth-rate in general increases as the concentration of cane sugar diminishes. The growth-rate is markedly greater in the solution of copper sulphate containing cane sugar varying in concentration from $m/4$ to $m/16$ than in the copper solution alone. This growth-rate was not a persistent feature, however, since in all the mixtures except that containing cane sugar at the least concentration, $m/16$, no growth took place in the second twenty-four hours. It appears, therefore, that when cane sugar is added in proper proportions, as in these experiments, the poisonous action of copper is somewhat diminished. This is probably due to the formation of copper saccharate and a consequent lessening of the number of Cu ions.*

As regards the effect of the addition of urea, $m/64$, it appears that the inhibiting action of the mixed solution is greater than that of the simple copper salt, the addition of the urea seeming to increase the total poisonous action.

COMPLEX MIXTURES

In order further to test the effect of additions of lighter metals to salts of the more poisonous elements, more complicated syntheses were made. These were of two classes: one mixed solution in which all of the salts present had a common anion; a second mixed solution in which the anion of the salt of the heavy metal did not appear in any of the compounds of the lighter

* See Loeb, J., and Gies, W. J. Weitere Untersuchungen über die entgiftenden Ionenwirkungen und die Rolle der Werthigkeit der Kationen bei diesen Vorgängen. Archiv für die ges. Physiologie, 93: 261. 1902.

metals. Mixtures were made in which, in addition to a copper salt, salts of sodium, magnesium, calcium and potassium, successively, were added. In every case, Ca excepted, the concentration in which each compound was present was that which, while distinctly retarding growth, still permitted it. We have, therefore, in every case, a salt entering into the combination in a concentration sufficiently great to be a distinctly toxic agent. The concentrations and other data in this connection appear in Table VI.

It will be noted in each case that the copper salt permits a slight growth. When the sodium salt is added, the mixture be-

TABLE VI

COMPLEX MIXTURES OF ONE HEAVY METAL AND AN INCREASING NUMBER OF LIGHTER METALS. AVERAGE GROWTH-RATES IN MILLIMETERS

With common anions									With different anions		
(*a*) Contents of Solutions	mol	Av. Growth 24 hrs.	(*b*) Contents of Solutions	mol	Av. Growth 24 hrs	(*c*) Contents of Solutions	mol	Av. Growth 24 hrs.	Contents of Solutions	mol	Av. Growth 24 hrs.
$CuCl_2$	65536	5.5	$CuCl_2$	32768	1.0	$CuCl_2$	65536	2.5	$Cu(CH_3.CO_2)_2$	65536	8.0
$CuCl_2$	65536		$CuCl_2$	32768		$CuCl_2$	65536		$Cu(CH_3.CO_2)_2$	65536	
NaCl	64	2.5	NaCl	64	1.5	NaCl	128	1.0	Na_2SO_4	128	3.0
$CuCl_2$	65536		$CuCl_2$	32768		$CuCl_2$	65536		$Cu(CH_3.CO_2)_2$	65536	
NaCl	64		NaCl	64		NaCl	128		Na_2SO_4	128	
$MgCl_2$	512	7.0	$MgCl_2$	512	2.5	$MgCl_2$	1024	6.0	$MgCl_2$	512	8.0
$CuCl_2$	65536		$CuCl_2$	32768		$CuCl_2$	65536		$Cu(CH_3.CO_2)_2$	65536	
NaCl	64		NaCl	64		NaCl	128		Na_2SO_4	128	
$MgCl_2$	512		$MgCl_2$	512		$MgCl_2$	1024		$MgCl_2$	512	
$CaCl_2$	32	14.5	$CaCl_2$	32	7.0	$CaCl_2$	64	9.0	$CaCl_2$	32	17.0
$CuCl_2$	65536		$CuCl_2$	32768		$CuCl_2$	65536		$Cu(CH_3.CO_2)_2$	65536	
NaCl	64		NaCl	64		NaCl	128		Na_2SO_4	128	
$MgCl_2$	512		$MgCl_2$	512		$MgCl_2$	1024		$MgCl_2$	512	
$CaCl_2$	32		$CaCl_2$	32		$CaCl_2$	64		$CaCl_2$	32	
KCl	128	19.0	KCl	128	5.5	KCl	256	10.0	KNO_3	128	22.0
Check		13.5			10.5			10.5			13.0

comes somewhat more harmful than the copper salt alone. The addition of magnesium to the mixture raises the growth-rate to a point beyond that reached in the copper solution, indicating a slightly beneficial antagonistic effect. When to these the calcium salt is added, the growth-rate immediately assumes practically normal proportions. This neutralizing or antitoxic effect of the calcium is very marked. When to the combination just referred

to the potassium salt is added, the growth-rate is still further increased. In the last mixture we have five salts, each, with the exception of the calcium compound, in a concentration strong enough to interfere distinctly with growth. As a result of their presence together, not only is there no addition of poisonous effects, but a neutralization of toxicity to such degree as to permit in the mixed solution a growth-rate equal to or greater than that seen in the check culture.

When the concentration of copper solution was doubled and the concentration of the other salts left as before, we found that the action of the copper was more slowly overcome, and even in the most complex mixtures studied, the growth-rate was still below that of the check. Apparently, the poisonous activity of the copper in these cases was greater than such as could be neutralized by the quantities of other salts added to it. When, on the other hand, the concentration of the copper solution was kept as in the first instance and the concentration of the lighter salts added was diminished by half, the neutralizing action of the latter was markedly less. In the most complex mixtures under these latter conditions the observed growth-rate only equaled that of the control. Apparently this fact was due to the unneutralized copper action, since each of the other salts present were below a harmful concentration.

Returning, now, to mixtures in which the anion of the copper salt is not duplicated in any of the other salts present, we see a result essentially like that just noted. When to copper acetate, for example, salts of the metals used before are added in quantities equal to those indicated in Table VI, a similar result is seen. The growth-rate in the pure copper salt in this case is somewhat greater, since the $CH_3.CO_2$ anion is slightly less poisonous than the Cl or the SO_4 anion. The addition of the sodium salt again increases the toxicity of the mixture. The further addition of the magnesium salt diminishes the harmful action somewhat, the activity of the mixture being, roughly, the same as that of copper acetate alone. The entrance of the calcium salt, as before, produces a marked acceleration of growth, the rate jumping to a point considerably above the control. The final addition of the potassium salt still further increases this stimulation. As a result of this ex-

periment it appears that it is immaterial here, as before, whether the lighter metals enter the solution in compounds containing an anion common to that of the heavy metal, or whether the anions be different.

DISCUSSION OF RESULTS

From the evidence at hand in these experiments it appears that, in solutions of salts, the conspicuously effective component of the molecule is the cation or the metal. This presumption, raised by the similar physiological effects produced by the cation of various salts of the heavy metals in equimolecular quantities, is strengthened by the action of mixtures containing a salt of the heavy metal with salts of lighter metals.

In case several salts having the same cation are mixed in solution the same lack of conspicuous influence on growth on the part of the anion is to be seen.* It is clear that the effect exerted upon the lupine roots by the salts of the heavy metals tested, differed according to the concentration of the salts. When sufficiently diluted, solutions containing copper, silver, mercury or zinc ions exerted a more or less clearly marked *stimulating* effect on growth. At a greater concentration, perhaps double that causing stimulation, a retarding influence was usually seen, and in a concentration approximately doubling this, growth was much interfered with; and on again doubling the concentration, little or no growth took place.

The effect of adding solutions containing Ca, Mg or Na ions was seen to vary with the character of the cation introduced. In mixtures containing but two salts (Tables III and VI) sodium seemed to show an increased poisonous action as though that of the sodium were added to that of the cation of the heavy metal. When to a solution of copper, a salt of magnesium was added, the mixture seemed to act with nearly the same intensity as the simple solution containing the copper in like quantity, exerting, therefore, little influence on the poisonous activity of the copper. When calcium was added, a marked reduction of the poisonous activity of copper ions was observed, a result seen even more strikingly in

* The physiological action of every dissociated salt in solution is doubtless an expression of the resultant biological effect of its component cations and anions. In these experiments the influence of the cations was predominant.

the case of zinc. Investigations by Swingle,* Clark,† Rumm and others on the action of Bordeaux mixture, although concerning very different proportions from those here involved, all testify to this power of calcium to neutralize the poisonous action of copper. Whereas the presence of calcium reduced the harmful effects of the copper to about one fourth of that seen in the simple copper solution, the antagonizing action of the calcium reduced the toxic action of the zinc to, at most, one sixteenth of that of the simple zinc solution. In the case of silver, the addition of calcium seemed to exert no ameliorating action. As far as the evidence at hand goes, it appears that such ameliorating action as was observed and would be expected stands in an inverse relation to the poisonous activity of the heavy metal.

From the above, as well as from the work of others, it appears conclusive that certain cations in mixed solutions exert a physiological action antagonistic to that exerted by other cations. The question next arises as to the nature of this modification and its seat. Does a mixed solution of calcium sulphate and copper sulphate or copper chloride, for example, produce the change (which brings about this physiological result) by affecting the condition of the copper in the solution outside of the cell, or does it bring about modifications within the cell itself? Is this antagonism an extracellular chemical change or an intracellular physiological change?

We have two sorts of cases to deal with. In the one case the salts have a common anion and in the other case the anions differ. We may set aside any such changes as the formation of double salts or the setting back of molecular ionization in the former case, since it has been shown that like results are seen when the mixed salts have common anions. This would seem to be a probable situation from *a priori* reasoning also, since in most cases the solutions of the salts of the heavy metals were so dilute that practically complete ionization took place. In that event, no matter what its associated anion was, the metal acted as free ions.

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* Swingle, W. T. Bordeaux Mixture. U. S. Dep. Agric. Div. Veg. Path. and Physiol. Bull No. 9. 1896.

† Clark, J. F. The Toxic Properties of some Copper Compounds with special reference to Bordeaux Mixture. Bot. Gaz. 33 : 26. 1902.

In the cases of our mixtures of salts having different anions, chemical reactions might be regarded as possible, with a consequent change in the forms of molecules. Here again, however, the great dilution of the salt of the heavy metal in our most important mixtures produced complete or nearly complete ionization, the heavy metal acting practically as free ions. We can then hardly regard changes of an ordinary chemical nature as being responsible for the differences in the physiological results. We think that interior physiological modifications are responsible for the observed differences in growth rate. This belief implies that the simple salt of the heavy metal and the mixture of this salt with that of a lighter metal, after penetration into the cell, affect the processes there being carried on in such a way as to bring about different results on cellular growth. In studying the effect on growth of simple solutions of copper and calcium salts, for example, we see that at the concentrations employed copper retards growth whereas the calcium salts greatly stimulate it. With each we have, in all probability, to do with antagonistic phases of physiological action. When we examine the results in cases like the above, it seems highly probable that the so-called antitoxic action of ions is due to different interior physiological modifications, and that the growth-rate observed in such experiments as these represents the physiological sum of oppositely acting stimuli, or of antagonistic protoplasmic changes.*

It has been shown that when salts of heavy metals are sufficiently dilute they exert a *stimulating* effect on growth, and when solutions of calcium and similar salts are concentrated enough, they hinder or entirely prevent growth, and may, in the case of the more soluble chloride and nitrate, prove fatal. Coupin † has shown that at different dilutions compounds exhibit *three distinct phases of physiological action*. When the solution is sufficiently dilute it seems too attenuated to produce any effect on growth. As the concentration increases, a *stimulating* phase is seen, which, on further concentration, passes over into the *retardation* phase—pronounced in proportion to the concentration.

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* Loeb and Gies, *l. c.*, 267.

† Coupin, H. Sur la toxicité du chlorure de sodium et de l'eau de mer e l'égard des végétaux. Rev. Gén. Bot. 10: 177. 1898.

In the mixtures of copper and calcium employed in our experiments, we may have had concentrations of each salt in different phases of action due to the degree of concentration. In $CuCl_2$, $m/65536$, we see that the Cu concentration is in the phase hindering growth, the resulting elongation of the root being about 3 mm. When $CaCl_2$, $m/128$, was tested, it was found to be in a concentration markedly stimulating when referred to the control in water, growing 20 mm. in the former case, against 14.5 mm. in the check. These opposite tendencies were brought together in the mixed solution with the result that the concentration (in terms of the copper salt permitting the growth-rate seen in the simple copper solution) moved up to approximately four times that observed in the simple copper solution. The stimulating action of the calcium seems to have operated against the retarding action of the copper, and the result is a marked diminution in the poisonous action of the copper.

The opposite result is seen in the mixture containing $CuCl_2$ and NaCl. The latter is in its growth-retarding phase until more dilute than $m/128$. Hence at $m/16$ it is in its growth-retarding phase, and when added to $CuCl_2$ at $m/65536$, likewise in this phase, the result is a sum of toxicity and an increased depression of growth-rate follows the combined action of the two. This also applies to the mixtures containing magnesium.

In considering the more complex mixtures of salts, indicated in Table VI, the chemical nature and influences of the resulting solutions are not readily determined. Much more concentrated solutions result in such mixtures with consequent decrease in dissociation. The probability that we are dealing with various kinds of non-ionized molecules, as well as with an indefinite number of ions, makes it impossible to speak definitely with confidence of the significance of our results in this connection. In general one may say that here, as in sea water, another complicated mixture of molecules and ions, the entrance of the calcium salt into the mixture is the stage in the synthesis at which the growth-rate approaches that seen in the check, and the final addition of the potassium salt seems further to increase the growth-rate. Or, in other words, all the salt solutions except the calcium entered the mixture in a concentration at which singly they would cause a

retardation of the growth-rate without bringing it to a standstill. Of the compounds present, therefore, the calcium salt only entered in a concentration representing the stimulus phase. The marked effect following the entrance of the calcium and the potassium may, in part, be due in these experiments to the cumulative increase of concentration of the solution, with the corresponding decrease in the rate of ionization and the diminished number of active ions. The fact that the potassium salt, although added in a concentration hindering growth when taken singly, increased the growth-rate when added to the mixture as its last member, seems to strengthen this supposition. Of course, changes of this nature represent changes in the solution itself and lie outside of the cell, and should not be confused with the mutually antagonistic intracellular action of ions in the case of very dilute solutions.

The Phyllodes of Oxypolis filiformis, a Swamp Xerophyte*

By Rosina J. Rennert

A large number of species of higher plants which live in ponds, marshes and other extremely moist habitats present structural characters of a xerophytic nature which have been most difficult of interpretation. A special study of the phyllodes of *Oxypolis filiformis* † was undertaken by the author in the hope that some additional light might be thrown on the subject. This work was carried on in the New York Botanical Garden under the direction of Dr. D. T. MacDougal, to whom I am indebted for valuable advice and fruitful suggestions.

Oxypolis filiformis is an umbellifer which grows in swamps and along the borders of ponds in the southeastern United States, as far north as Delaware. The leaves exhibit curious modifications by which they depart widely from the uniformly broad or widely dissected umbelliferous type, being reduced to stiff grayish-green awl-shaped phyllodes, which have a structure as if made up of a number of sections of varying lengths, the joints being distinctly noticeable and marking the position of peculiar septa in the interior tissues. This habit of the leaves gives the plant a rush-like appearance, an effect which is heightened by the small size of the cauline, and the strong development of the basal phyllodes. The entire phyllode is flattened along one side. A minute pit is to be observed externally to every septum, occurring in the middle of the slightly flattened surface.

Briquet ‡ has given a detailed account of the results of his examination of this plant with respect to the anatomy of the phyllodes. He describes the epidermis as a single layer of cells with curved outer walls protected by a thickened outer membrane and a folded cuticle. The stomata were noted as either flush with the

* Read before the Botanical Society of America, by invitation, at Pittsburg, Pa., July 1, 1902.

† Oxypolis filiformis (Walt.) Britton. *Tiedemannia teretifolia* (Muhl.) DC.

‡ Briquet, J. Etude de la feuille du *Tiedmannia teretifolia* DC. Bull. Herb Boiss. 5: 461–465. 1897.

surface, or sunken slightly below, being about 48 to 54 μ in length. Directly underneath the epidermis is a hypoderm composed of small sclerotic cells with a small lumen. The hypoderm is one to three layers in thickness, and is interrupted only underneath the stomata. The chlorophyl-bearing tissue consists of three to six layers of cells, the outer ones of which are palisaded. The innermost layers are more loosely arranged. Internal to the chlorophyl-bearing cells is a cylinder of four or five layers of large thin-walled cells, designated as endoderm by Briquet. The fibro-vascular bundles are situated in this tissue. The pericycle comes into contact with the chlorophyl-bearing tissue in places, however. The axial portions of the phyllodes were found to consist of thin-walled stellate elements which are in contact at the tips of the rays. The septa were found to be composed of sclerotic cells with numerous branching canals extending radially through the walls. The fibro-vascular bundles are unbranched in the intervals but break up at the septa and form a mesh of anastomosing branches, which however do not traverse the septa radially to any great distance.

Briquet explains the seemingly anomalous possession of transpiration-hindering hypoderm by this marsh plant by the fact that it is subject to two extremes of conditions. The mechanical advantages from the cylindrical form of the phyllodes, and the aërating capacity of the stellate tissue would be of advantage during the early spring season, when the plant is more or less submerged. The shape of the leaf would present a reduced surface and the hypoderm would check transpiration during the mid-summer season after the waters have subsided.

My own examination of this plant and the results of the experimental tests made with it have revealed some structural features not mentioned by Briquet, and lead to a somewhat different interpretation of its adaptative features.

Some plants brought from Georgia and Florida in 1901 and 1902 were grown in the greenhouse under various conditions as described below. The septa in the phyllodes of these specimens were found to consist chiefly of small thin-walled cells containing chlorophyl, and resembling the elements of the other chlorophyl-bearing tissue, with only an occasional thick-walled sclerotic cell. The endoderm was found to be continued on the surfaces of the

septa. I am not able to account for the difference in these septa as observed by Briquet and myself, except to suggest that his plants were grown under conditions which induced the sclerosis of the elements of the septa and which he has not described.

The most important additional fact concerning the structure of these organs, however, is that all of the specimens in the herbarium of the New York Botanical Garden, and of those cultivated by myself in the open, exhibit the pits or depressions mentioned above, and this feature is to be seen even in the first leaf of the seedlings. These pits seem to be the external openings of oil or resin glands which are situated immediately below each septum. The pit is partly closed by a chlorophylless outgrowth of the lower margin, which can be distinguished by the unaided eye as a minute scale. Goebel * describes similar outgrowths on the phyllodes of *Crantzia linearis*, an umbellifer of the same habit as *Oxypolis*, and despite the fact that they occur along one side of the leaf only, he holds the opinion that they are vestigial leaf-divisions. This conclusion can hardly be valid with respect to the pits and scales of *Oxypolis*. These formations are absent from the basal septa as they would be if vestigial leaf-divisions, but as a matter of fact the scales and pits originate on a line ninety degrees from the plane of the stipules. Furthermore the specialized structute of the formations in question militates against their acceptance as vestiges.

It was found that the floor of the pit is on a level with the plane of the diaphragm. It is this floor and the flap which closes the orifice only, whose structure indicates a specialization of function. With these exceptions the invagination is lined by a continuation of the normal epidermal cells of the phyllode, covered by a cuticle continuous with that on the outside of the leaf. The floor and flap have an epidermis of smaller cells the outer walls of which are slightly convex, forming small papillae. No cuticle is present. The small openings which occur in this epidermis measure about 19 μ in diameter and are formed by two cells broadly elliptical in shape. Directly below these epidermal cells and making up the greater part of the flap is a mass of irregularly shaped cells dovetailed compactly into each other. The epidermal cells as well as the cells of this tissue contain a great amount of resin or oil. En-

* Goebel, K. Organographie der Pflanzen, 494. 1901.

larged tracheae are to be found in great numbers leading into this compact tissue and forming a solid mass below it. The anastomosing bundles of the septa end here. In the light of this peculiar

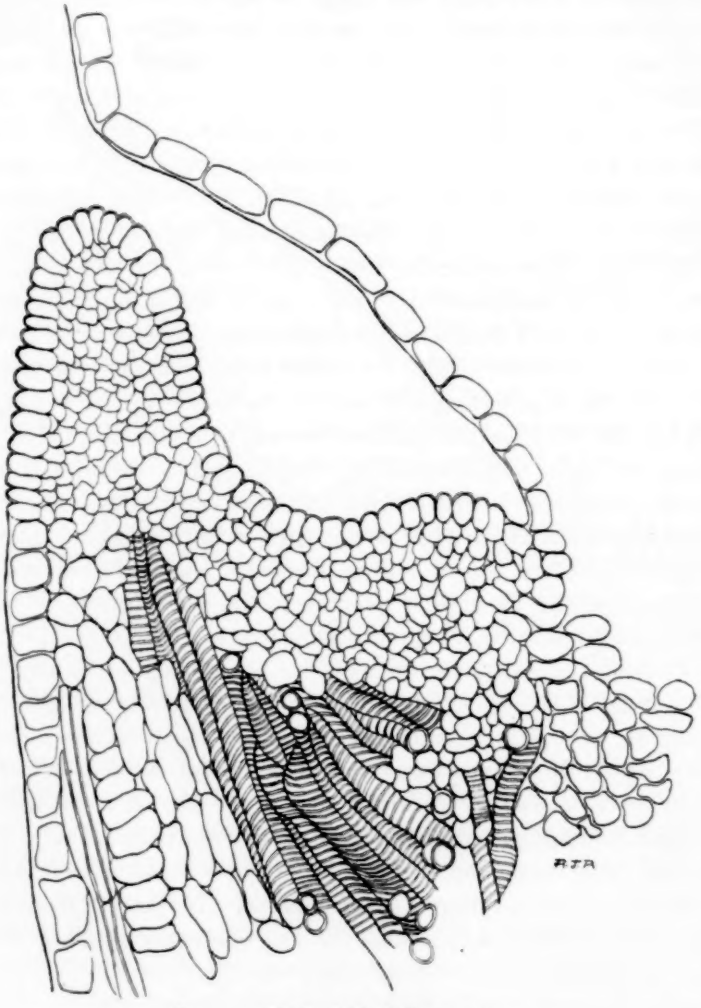

FIG. 1. Oil-gland of phyllode, × 140.

structure, it seems reasonable to regard these pits as glands for the secretion of oil or resin.

In opposition to Briquet, I am led to the conclusion that *Oxy-*

polis does not owe its peculiar structure to an adaptation to wet and dry periods, but that it is a true swamp or bog xerophyte in accordance with the generalization of Schimper, who supposes that the water of bogs and swamps contains such a large proportion of humic acid as to render absorption difficult. Plants growing in such places therefore have difficulty in securing a requisite supply, as if growing under arid conditions. Not all plants are capable of absorbing water from a mixture exhibiting a higher pressure than that of the cell-sap of the absorbing organs.

Dr. Shaw * has pointed out that the vegetation of a pond in its final stage is always xerophytic and has drawn attention to the fact that the continual deposit of organic material around the margin of a pond will produce a zone so much filled with humic acid as to be entirely devoid of vegetation. Dr. Cowles † has upheld this view of the xerophytic character of an undrained swamp and has frequently noted the remarkable assemblage of xerophytic adaptations such as leathery or hairy leaves and special structures for water absorption exhibited by the flora of peat bogs. In confirmation of this standpoint Dr. Cowles has pointed out that if plants growing in swamps of this type are xerophytic we ought to find them thrving in dry regions. And this he reports to be true; *Clethra alnifolia*, *Spiraea tomentosa* and *Myrica cerifera*, generally conceded swamp plants, have been found thriving and in all respects normal on dry hillsides.

As Briquet has indicated, the most superficial examination of the plant brings to light the unmistakably xerophytic character of the reduced leaf-surface and the strong development of hypoderm. On the other hand many of the characters which Briquet regards as demonstrating the hydrophytic nature of the plant, seem when viewed in the light of recent ecological work, to be adaptations either for water storage or the prevention of transpiration. The large thin-walled empty celled endoderm certainly exhibits capacity for water storage. The thick cuticle and the waxy incrustation of the epidermis, the accessory cells and the sunken position of the stomata, and the presence of resin glands all point to the con-

*Shaw, C. H. The Development of Vegetation in the Morainal Depressions of the Vicinity of Wood's Hole. Bot. Gaz. 33: 437. 1902.

†Cowles, H. C. Bot. Gaz. 27: 293. 1899.

clusion that the conservation of water is the chief purpose met by the striking structural adaptations.

This view is strengthened by the experimental results. Two series of cultural tests were made. In one series a number of plants in pots of soil were enclosed in bell-jars and were thus grown in a saturated atmosphere. Others were entirely submerged in

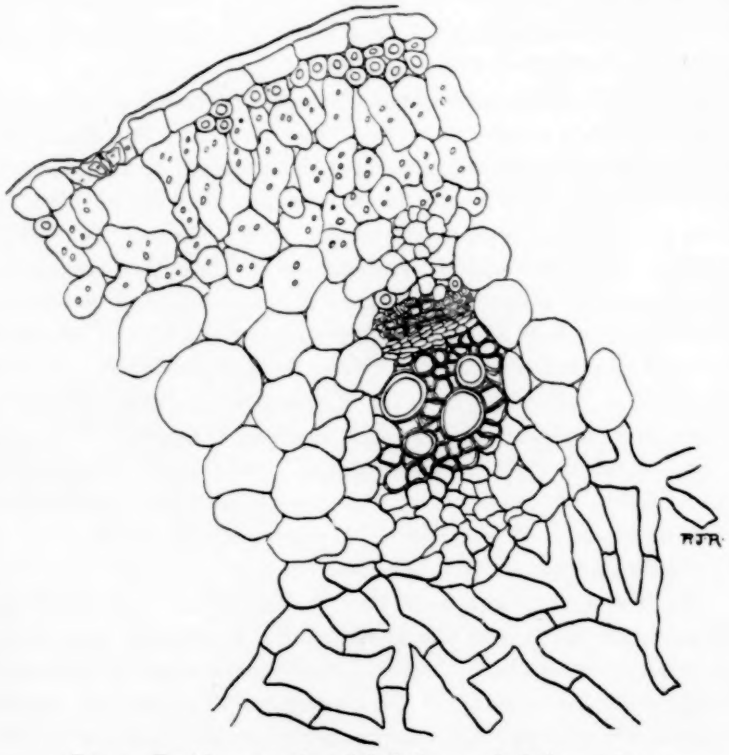

FIG. 2. Partial cross-section of phyllode, xerophytic form, × 140.

tanks of water. The phyllodes produced under these conditions were similar. In both cases these organs were delicate, hollow, terete, translucent, light green in color, and exhibited no trace of glands or pits. The stipules were membranous and reduced in width. The epidermal cells were without wax or cuticle and were greatly elongated longitudinally. The stomata were partly exserted and were of a reduced number, but retained their characteristic structure. In consequence of the regularity of the epidermal

rows of cells, the stomata occurred in definite rows separated from each other by five sterile epidermal rows. Hypoderm was absent. The chlorophyl-cells followed directly upon the epidermis. This tissue was reduced to about three rows, and the palisade character of the first row of cells was not very marked. The endoderm was also less developed. It consisted of only one to three rows of cells. The stellate tissue of the other form was entirely absent here. As a consequence of the meager development of endoderm the fibro-vascular bundles jutted out into the central cavity. The xylem in the bundles was reduced and the position of the resin duct changed. In the normal type it was always to be found outside of the phloëm; in these phyllodes it was on the other side of the bundle near the xylem. This position of the duct has been

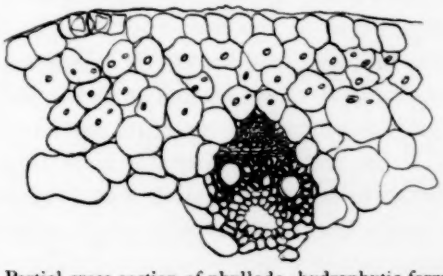

FIG. 3. Partial cross-section of phyllode, hydrophytic form, × 140.

pointed out by Van Tieghem as more primitive or juvenile. The diaphragms were composed entirely of thin-walled cells and the anastomosing bundles contained in them were much weaker and, contrary to the habit in the solid phyllode, anastomosed as freely at the center of the septum as about the edge. No trace of glands in the phyllode have been found and there is consequently no general convergence of bundles toward any single point in the margin.

The phyllodes of the submerged plants possessed in all cases the same structure as those grown under the bell-jar and exhibited an additional modification in their method of propagation. New plants were developed from the nodes of the xerophytic stems which had been developed before the plants were submerged and also in turn from the nodes of plants produced under water.

The water in which the immersed plants were grown presented

none of the difficulties of absorption of the liquid in bogs. These submerged individuals as well as those in the bell-jars were seen to undergo true aquatic adaptations consisting in the loss of hypoderm of the central stellate tissue and of the glands; the reduction of the chlorophyl-bearing elements, of the endoderm, and of the number of stomata as well as of the xylem; the change in the position of the resin duct; the modification of the epidermal cells, stomata, cells of the septa and the course of the bundles through the septa; and the adoption of a new method of propagation.

These changes may be divided naturally into two classes, those which involve a suppression of xerophytic characters and those which are a means of adaptation to moist conditions and therefore hydrophytic in their nature. In the first class we must consider the loss of hypoderm and glands, the reduction of palisade-cells and water-storage tissue of the endoderm and the loss of cuticle; while we find in the modification of the epidermal cells, the reduction and modification of the stomata and the adoption of a new method of propagation types of structure peculiarly distinctive of hydrophytes. If the action of water free from high concentration of osmotic substances will induce such sweeping departures from the normal, it seems but reasonable to conclude that the plant is naturally a swamp xerophyte.

The adaptations described seem to have been most thoroughly adopted by the species since the characteristic structure of the phyllodes is to be found in the seedlings. These seedlings were raised from seed developed by the plants with which the experiments were made. The cotyledons were flat and linear in shape and 5 to 6 cm. in length. When the first leaf developed it exhibited the typical awl-shaped, septate character and bore glands and the accompanying scales along one side throughout its length. In internal structure it also resembled the later leaves in all respects, except that the hypoderm was absent and that the cells of the endoderm bore chlorophyl.

The chief results of importance brought out in the foregoing paper may be briefly summarized as follows:

1. The leaf-structures of *Oxypolis filiformis* are terete, awl-pointed phyllodes with numerous septa or diaphragms, and this form is exhibited even by the first leaf of the seedling. The

structure of the septa as examined by myself differs notably from that described by Briquet.

2. The phyllodes normally bear numerous glands sunk in pits which are edged with a minute scale. These glands are on a line at 90° from the plane of the stipules and the attendant scales may not be considered as vestigial leaflet structures as suggested by Goebel as to the scales of *Crantzia*.

3. Plants of *Oxypolis filiformis* when grown in a saturated atmosphere or under the influence of normal soil-water (submerged) exhibits marked hydrophytic adaptations of the phyllode. The changes ensuing under such circumstances emphasize still further the xerophytic character of the phyllodes as indicated by their anatomical character, and reënforce the conclusion that this species should be regarded as a swamp xerophyte.

Some common Types of Lichen Formations

By Bruce Fink

In a paper published about three years since by the Torrey Botanical Club, I referred to the lack of adequate consideration of the ecologic distribution of lichens and attempted to outline briefly some of the interesting questions which may well claim the attention of lichen collectors. It is my purpose in this paper to take up some of the ecologic factors there suggested and follow them out in considering four or five of the more common types of lichen formations that have come to my notice in field work.

In attempting such a presentation I am well aware that there is much yet to be ascertained concerning the influence of physical structure and chemical composition of substrata upon lichen distribution. It is well known that those foliose lichens which have rhizoids are especially adapted to rough and loose surfaces, while the smoother and more dense surfaces usually bear lichens having more rudimentary crustose thalli. As to the influence of chemical composition of substrata in determining the composition of lichen formations, M. Fünfstück has studied the fatty secretions of calcareous rock-lichens and finds that these fats are probably utilized by the plants for nutrition. Hence, as these plants seem to build up fats from the carbonates of the rocks, they would doubtless have an advantage over other lichens in the struggle for possession of the calcareous rocks. That these and other rock-lichens secrete acids that cause the rocks to decay, rendering them easy of penetration, is well known, and G. Lindau finds that crustose bark-lichens act in much the same way in gaining possession of the smooth bark on which they commonly grow.

To what extent these lichens utilize the elaborated sap of the tree for nutrition we do not know, and definite knowledge in this matter would assist greatly in ecologic studies. In general, lichens are known to produce certain chemical compounds, varying more or less with the nature of the substratum. In what degree these compounds are of use to the plants and to what degree they are derived from the substratum are little known. Till these prob-

lems are solved, we can hardly hope to discuss very intelligently chemical composition of substrata as an edaphic factor.

On the other hand the anatomical structure of lichen thalli is fairly well known, so that structural adaptations may be more intelligently considered. Moreover, a large amount of observation has shown conclusively that many lichens commonly occur upon substrata of quite varied chemical composition and physical structure provided the conditions of light and moisture are favorable. Therefore, all things considered, the structural adaptations of lichens to these conditions must for the present receive chief attention in any consideration of lichen formations.

With this much of preliminary statement, I shall follow out the consideration of four or five of the commoner kinds of lichen formations. Doubtless the first to present themselves to the average collector would be what I have, in my studies of the Minnesota lichens, seen fit to call the *Parmelei formations of trees with rough bark* and the *Pyrenula formations of trees with smooth bark*. The lichens composing these formations are the ones best known and most collected, and I shall not reproduce here the rather laborious list of plants most commonly found in them, such lists having already appeared in the Minnesota Botanical Studies. However, the lichens growing more or less commonly on rough bark vary widely as to structural adaptations. The typical members of such formations are the species of *Parmelia* and their near relatives in *Theloschistes* and *Physcia*. The lichens of these three genera commonly have foliose thalli, not very closely adnate, and possessing rhizoids for attachment and support and secondarily for absorption of moisture. These thalli have good cellular cortices on all sides, serving both for support and for protection against excessive evaporation. Scarcely less at home in these formations are the fruticose species of *Ramalina* and *Usnea*. These plants also have well-developed cortices, which serve for protection against excessive evaporation and also give mechanical support so that the plants are able to rise from the substrata or to hang in pendulous fashion. The foliose species of *Leptogium* with thin upper cellular cortices only, seek damp places in the formations and the species of *Collema* devoid of cellular cortex, yet more moist habitats.

Of the lichens of the smooth bark formations, the species of *Py-*

renula are most representative. These plants have very rudimentary thalli, consisting mostly of a network of hypophloeodal hyphae in which are entangled the algal cells. In gaining a foothold, the hyphae seem to work their way between the decaying cells of the bark, and, once firmly established below the surface, the bark itself furnishes both protection and support, as well as moisture. After *Pyrenula* the species of *Graphis* and *Arthonia* contain the next most typical members of smooth bark lichen communities. In these two genera, the thalli are of essentially the same structure as in *Pyrenula*.

The crustose species of *Biatora*, *Buellia* and *Lecidea* all have small thalli devoid of cellular cortices. But these plants have, as is commonly true of the more rudimentary epiphloeodal thalli, an upper colorless network of hyphae devoid of living algal cells and tending to lie in a horizontal direction. These hyphae, together with a number of entangled dead algal cells, form more or less of a protection to the living algae below. The lichens having such thalli may be looked for in either the smooth or the rough bark formations, and the same is true of certain species of *Lecanora*, *Placodium* and *Pertusaria* which have larger thalli, possessing at least some indication of upper cortex.

In the above statements I have had in mind the bark formations of our common deciduous trees, and such lichen assemblages may be looked for wherever these trees exist in considerable numbers in forests. Yet no American has seriously studied the relations of epiphyte or parasite to host, though statements may be found in scattered writings regarding the occurrence of certain lichens upon a given species of tree. In Europe, F. Arnold, in his systematic studies of the lichen flora of Munich, Germany, and of that of the Jura Mountains, has exhaustively recorded the lichens growing upon each species of tree and has extended the study to other substrata than trees. This is interesting, especially regarding those lichens that are confined to a particular host or substratum, but Dr. Arnold has left practically untouched the more interesting and obscure problem of the adaptations of the lichens to these substrata.

Passing from these lichen formations of the trees, let us next give attention to what appear to be the next most easily observed

of lichen formations of our northern prairies, viz., those of the bowlders. I shall give a list of the lichen species most commonly occurring in such formations and shall designate the formations thus:

THE LECANORA FORMATIONS OF EXPOSED BOWLDERS

Physcia stellaris (L.) Tuck.
Physcia caesia (Hoffm.) Nyl.
Placodium cerinum sideritis Tuck.
Placodium vitellinum (Ehrh.) Naeg. & Hepp.
Lecanora rubina (Vill.) Ach.
Lecanora varia (Ehrh.) Nyl.
Lecanora cinerea (L.) Sommerf.
Lecanora fuscata (Schrad.) Th. Fr.
Rinodina sophodes (Ach.) Nyl.

This short list includes only about one third or one fourth of the lichens that may commonly occur in the formation in a locality where it is well developed; but the few given may be looked for in any favorable locality in the northern United States, and the addition of other species would scarcely show any greater amount of variation as to adaptations. Indeed, it will be sufficient to consider the adaptations of the genera of the above list rather than those of each species. The species of *Lecanora* and *Placodium* are the most characteristic plants of such formations. The species found on exposed bowlders are nearly all strictly crustose and closely adnate, so that moisture is confined in the substratum below the thallus and readily absorbed. The larger species of *Lecanora* usually have well developed upper cortices for protection against excessive evaporation. The species of *Placodium* have upper cortices more or less developed, and some of the species have such structures below as well. The species of *Physcia* are foliose, but closely adnate; and those commonly found in these exposed formations have well developed cellular cortices on all sides. *Rinodina* has a small thallus, consisting of a tangle of hyphae enclosing the algal cells and protected only by the upper more or less horizontal layers of hyphae and the entangled dead algal cells. In general, those plants of such formations which have no upper cortices have very small thalli, while those having the

cortical protection and support may attain a quite considerable size even in their exposed habitat. A large foliose lichen devoid of cellular cortex, as a *Collema*, could hardly exist in the formation. Finally among the lichens of such formations are a few foliose species with well-developed cortices on all sides, but still closely adnate; and a much larger number of crustose forms which have upper cortices only or none, and which, though epilithic, are closely adnate and have small thalli.

I have recorded from some Minnesota localities what I have called *The Mixed formations of shaded bowlders.* I cannot discuss these rarer formations within the limits of this paper, but merely wish to refer to them as being quite distinct from the exposed bowlder formations. Finally, before leaving this portion of the subject, I may state that the formations of extended rock exposures will not be found to differ greatly from those of the closely related bowlders, except where influenced by climatic conditions due to proximity to large bodies of water along the coasts or on the shores of the great lakes, or to high elevation in the mountainous regions.

The three classes of lichen formations thus far discussed are the ones which may be most easily investigated in the field, and yet there are two more types which are so easily studied in many parts of our territory that I am disposed to give them some attention. I refer to the formations of exposed calcareous earth and to those of exposed calcareous pebbles or horizontally exposed limestone. In a previous study, I have designated the first of these formations thus: *The Biatora decipiens formations of exposed calcareous earth.* These formations are remarkably constant as to the elements composing them wherever I have observed them in Minnesota, Iowa and Illinois, and are likely to contain the species listed below, and few if any others, wherever well developed in the northern states. The list of species is:

Heppia Despreauxii (Mont.) Tuck.
Urceolaria scruposa (L.) Nyl.
Biatora decipiens (Ehrh.) Fr.
Biatora decipiens dealbata Auct.
Biatora muscorum (Sw.) Tuck.
Endocarpon hepaticum Ach.

These formations are commonly best developed on hillsides where the plants are washed by lime-impregnated water which flows down the slope during rains. As to structural adaptations to an exposed and usually dry environment, the plants all have small thalli and are closely adnate. The thallus of *Biatora muscorum* (Sw.) Tuck. is very small and devoid of cortex. That of the *Urceolaria* is somewhat larger and has a pseudo-cortex above. The other larger thalli furnish good protection to the algal cells within, that of *Biatora decipiens* (Ehrh.) Fr. having a very heavy cellular cortex above, that of *Endocarpon* being provided on all sides with a well-developed cortex while that of the *Heppia* is cellular throughout. These cellular areas of the larger thalli serve of course not only for protection against excessive evaporation, but also for support. It must be said that none of the thalli of this formation are really large, those of the three last considered averaging from 3–6 mm. in diameter. Indeed a large lichen thallus found in such a formation would needs be considered as an accident in distribution.

Closely related to the formations of calcareous earth and usually occurring with or near them, are those of the calcareous pebbles or horizontally-disposed calcareous rocks. Taking the name partly from a lichen which I have thus far never failed to find whenever the formation is well developed and giving a list of species commonly found in such formations, we have the following :

THE LECANORA CALCAREA CONTORTA FORMATIONS OF EXPOSED HORIZONTAL LIMESTONE SURFACES (OR OF LIMY PEBBLES)

Placodium vitellinum aurellum Ach.
Lecanora calcarea contorta Fr.
Lecanora privigna (Ach). Nyl.
Endocarpon pusillum Hedw.
Verrucaria muralis Ach.

These formations are less constant as to floral elements than those of calcareous earth and when well developed usually contain several variable elements not given in the above list. The lichens composing such formations have small thalli, closely adnate or even more or less strictly hypolithic. All except the hypolithic

Verrucaria and *Lecanora privigna* (Ach.) Nyl., which has a very evanescent as well as rudimentary thallus, have more or less developed cellular or pseudo-cellular cortices above. These upper cortices give the small thalli sufficient protection against evaporation, thus adapting them to their xerophytic habitat.

The occurrence of the fatty secretions in some of the lichens of the last two formations should be noted as an adaptation to their calcareous substrata. Also it may be stated that all but one of the types of lichen formations recorded in this paper are essentially xerophytic, for I suppose that the lichen formations on rough bark in mesophytic woods may be regarded as xerophytic at least as regards the more typical foliose and fruticose members. The one exception is the formations of the smooth bark, at least when borne hypophloeodally on trees with living bark so that moisture passes readily from the trees to the lichens growing upon them.

The five types of lichen formations considered in this paper have been selected from some twenty-five that I have observed in the field. Ecologic distribution of lichens is an extremely interesting field of botanical study, and my object has been to indicate, by preliminary statement followed by application to some common types of formations, what may be accomplished in this line by careful investigation.

FAYETTE, IOWA.

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